

THE CHEMICAL SENSE AND FEEDING BEHAVIOR OF *NEREIS VIRENS*. SARS.

MANTON COPELAND AND H. L. WIEMAN,

MARINE BIOLOGICAL LABORATORY, WOODS HOLE, MASS.

In 1873 Verrill stated in his report on the invertebrates of Vineyard Sound that the clam worm, *Nereis virens*, "feeds on other worms and various kinds of marine animals. It captures its prey by suddenly thrusting out its proboscis and seizing hold with the two terminal jaws; then withdrawing the proboscis, the food is torn and masticated at leisure. . . ." Maxwell (1897) confirmed Verrill's conclusions as to the character of its food. He found that if a small piece of worm on the end of a needle is placed within reach of a normal *Nereis*, the animal seizes the food and devours it. More recently, however, Gross (1921) has failed to find any evidence that *Nereis virens* is a carnivorous worm; concluding that it feeds principally upon plant life. This verdict was based upon studies in the laboratory and in the field.

Our own observations began with dropping crushed periwinkies [*Litorina littorea* (Linn.)] in shallow water at low tide in order to study the responses of crustaceans. That such bait would cause *Nereis* to react was a thought that had not occurred to us, so that our surprise can easily be imagined when presently a worm extended the anterior end of its body from below smooth sand, moved toward the snail, seized and quickly jerked it down into its burrow. What we saw was a confirmation of Verrill's statement noted above.

Subsequent tests with the same food resulted in numerous responses of a similar nature until it appeared that *Nereis* was reacting with remarkable precision to small amounts of materials emanating from the crushed snails. A worm usually emerged several centimeters from the snail, and advanced rather slowly over the surface of the sand by movements of the body and parapodia toward the bait, which it finally seized in its powerful jaws and drew rapidly to its burrow by a sudden

muscular contraction. *Nereis* responded in the same way to all other forms of animal food which were offered, viz., crushed clam [*Mya arenaria* Linn.], mussel [*Mytilus edulis* Linn.], bits of fish [*Fundulus heteroclitus* (Linn.)], and meat of the blue crab [*Callinectes sapidus* Rathbun]. When the food was grasped it was always pulled to the mouth of the burrow and, unless too large, into the interior of the burrow itself. In no case was a worm observed to leave the burrow entirely and move about freely in the water.

In order to learn something of the extent to which the animals depend upon a chemical sense in such reactions a number of tests were made, one of which was carried out in the following manner. The position of a worm was first determined by baiting with a piece of clam which was removed before the animal had a chance to seize it. Some fragments of the same food were then wrapped in cheese cloth and dropped into the water about five centimeters from the opening of the burrow. Equidistant from the burrow and one centimeter from the first packet was placed a second, consisting of a white pebble done up in cheese cloth. Each packet measured slightly over two centimeters in diameter and both had essentially the same appearance. The worm soon responded by emerging from the burrow and, advancing in a straight line toward the baited packet, seized it and dragged it down almost out of sight. The packet was then dug out and replaced in its former position. In a few minutes the worm reappeared and repeated the reaction in every detail. Again the food was recovered, and this time the positions of the baited and unbaited packets were interchanged. Within several minutes the anterior end of the worm came out of the sand somewhat nearer to the packets than before and moved forward in a course which, if adhered to, would have brought it between them. However, when close to the packets the animal suddenly turned and fastened its jaws in the baited one and for the third time pulled it into the sand.

The results of this experiment indicate that sight plays little or no part in the worm's food reactions under the conditions prevailing. Tests were also made by dropping pebbles near occupied burrows to ascertain if agitation of the water, or some

physical factor, influenced the animal's response. To such stimuli no response occurred, although the worms appeared promptly when crab's meat was placed in the same situations. The evidence, therefore, supports the view that a chemical sense is the primary one upon which its responses to animal food depend.

Certain striking features of recorded behavior may now be considered. It was early noted that when a worm appeared from beneath the sand in response to chemical stimulation there was little uncertainty shown in the direction of its movements. Almost invariably it advanced toward the bait which, if not too far away, was generally found without difficulty. It was also observed that, when the food was out of reach, the worm withdrew into its burrow only to reappear, frequently in a position nearer the source of the stimulating material. In order to study these directive reactions further a number of animals were collected and brought into the laboratory. They were kept for a time in dishes containing water and sea lettuce, and under these conditions they would often take from forceps small pieces of meat offered them. In fact, all of the foods to which the worms reacted in their natural habitat were also accepted as they moved about in the folds of sea lettuce, enclosed more or less by mucous secretions. Under these conditions, however, they were easily disturbed and their somewhat erratic feeding behavior indicated that they were unfavorably situated for any detailed experimental study of their chemical reactions. Accordingly four worms were placed in a circular glass dish having an inside diameter of 28 cm. and containing sea water and sand. The layer of sand was approximately 2.5 cm. deep. The animals immediately entered the sand, forming burrows lined with mucus which here and there connected with the surface by well marked openings. They showed no tendency to leave the burrows if the dish remained undisturbed. After preliminary tests, which demonstrated that the worms would react to food juices as readily as they did in their natural surroundings, three similar experiments were performed, one of which is described in some detail in the following paragraphs.

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9:32:00 A. M. The water was gently stirred with a glass rod and the dish kept under observation for ten minutes. The worms remained in the sand.

9:51:00. A clam (5.4 cm. in length) cut up on half shell was placed in the center of the dish and the water stirred as before. The worms appeared as follows: worm I at 9:52:15, seven centimeters from the edge of the dish; II at 9:53:17; III at 9:54:45; IV at 9:56:50. Worms II, III, and IV appeared at the periphery of the dish.

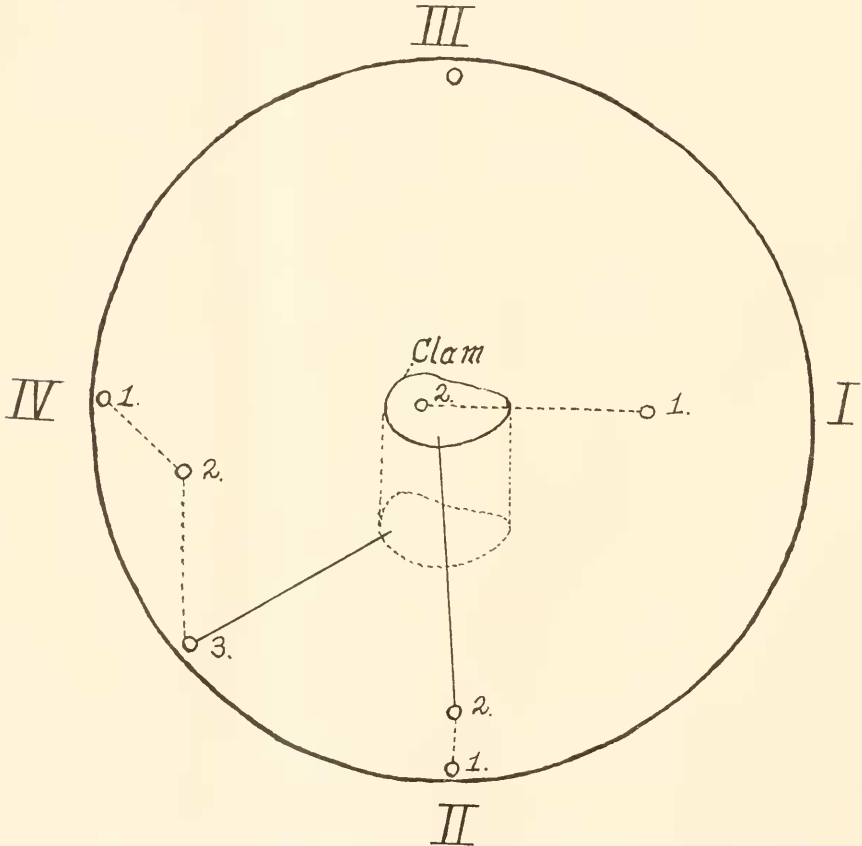


FIG. 1. Illustrating the responses of worms I., II., III., and IV., described in the text. The arabic numerals denote successive appearances of individual worms.

Worm I.—At its first appearance it made a few wavering movements with the anterior segments of its body at the mouth

of the burrow and then withdrew. The same reaction was repeated a few minutes later. Finally at 10:07:30 it was found with its head exposed directly beneath the clam to which point it had burrowed, a distance of 7 cm.

Worm II.—It repeated its first appearance at the edge of the dish, withdrawing quickly each time. At its third appearance the worm proceeded directly toward the clam, exposing about 10 cm. of its body, and then quickly disappeared within its burrow. At 9:59 it came out of the sand 2 cm. nearer the clam, stretched out until it reached the clam, but finding a small fragment nearby, it seized the fragment and withdrew without disturbing the clam. At 10:07:30 the worm again emerged, this time within 2 cm. of the clam, which it grasped and dragged a distance of 3 cm., partially burying its prize in the sand. When the clam was dislodged the head of worm I. was disclosed directly beneath. At 10:13:30 worm II. reappeared at the mouth of its original burrow at the edge of the dish but made no effort to reach the clam.

Worm III.—Emerging first at the edge of the dish it immediately moved toward the clam, not quite reaching it. After withdrawing it came out again at the same point at 10:11, but by this time the clam had been pulled 3 cm. away by worm II. It drew back into its burrow and was not seen again.

Worm IV.—When first noted at the edge of the dish the worm made a few wavering movements and then disappeared, coming up again for a short time 3 cm. away. Finally at 10:17:30 it was observed at the edge of the dish, but 10 cm. from the first opening. It advanced directly toward the clam, seized it but failed to move it because of the position in which it had been wedged in the sand by worm II. After tugging at it a while, and probably biting off a piece, the animal withdrew.

The results of this experiment and two others carried out in the same way confirmed beyond question our observations made in the field. Although a worm on coming to the mouth of its burrow usually advanced the anterior end of its body in a direction toward the clam, it perhaps showed somewhat less certainty in this phase of its response than when in its natural environ-

ment. This, however, was to be expected, for in the dish well defined water currents bearing food juices, which undoubtedly aid under natural conditions in directing the animal toward the food, were largely absent, and the stimulating material must have become rather generally distributed through the water. The animals, nevertheless, after stimulation, instead of confining their activities to the periphery of the dish, near which they usually appeared, exhibited a marked tendency on failing to reach the clam to move toward the center of the dish. The explanation of how the worm maintains its direction toward the source of stimulation after withdrawing into the sand is not clear. It appears likely, however, that this directive response is a movement toward areas where the chemical substances given off by the food, and infiltrated through the sand, show higher concentration. The sense of sight plays an insignificant if any part in these reactions, for if a pipetteful of filtered clam extract is substituted for the clam in an experiment like that just described, the worms show the same responses, extending their bodies toward the center of the dish where the extract was placed.

In the laboratory as well as in natural surroundings we never saw the animals lose contact with their burrows during their movements over the sand in response to food excitation. They were tested by moonlight in the laboratory with food but no difference from behavior in daylight was noted.

For some time after the first observations on *Nereis* were made we were unable to explain how the stimulating material derived from the small quantity of food used in some of our experiments penetrated the burrows in sufficient amounts, and quickly enough, to call forth such prompt reactions. The solution of this problem was found when worms were allowed to enter glass tubes, open at both ends, the calibers of which were nearly the same as those of their burrows. Tubes of this sort are soon lined with mucus and the worms remain in them for hours at a time, exactly as they do in the sand. No difficulty was experienced in inducing them to enter the tubes. It was only necessary to direct the head into the opening, after which the worm moved forward of its own accord; and once well inside stopped locomotion. In the tube *Nereis* exhibits a most striking

form of behavior which may be described as a rhythmic undulatory movement of a portion of the body taking place in a dorso-ventral direction, the parapodia remaining passive. These muscular waves were sometimes limited to the anterior end, in which case a nodding of the head occurs; at other times they appeared only at the posterior end, or perhaps in a position nearer the middle of the body. The movement is not interrupted but never discontinued for any length of time. This activity produces a current in the water which passes along the animal's body from the anterior to the posterior end.

That these body movements also occur when the animals are in their burrows was clearly demonstrated by two individuals kept in glass dishes containing sand. In one instance the nodding of the head mentioned above was seen through the glass as the animal lay in its burrow at the side of the dish. Carmine grains dropped in the water a few centimeters above an opening of the burrow were immediately drawn inside. In another case a long burrow was formed against the glass and here the undulatory movements of the worm were distinctly visible. From this burrow three tunnels led to openings at the surface close to the glass. From this it is clear how *Nereis*, concealed in its passageways within the sand, receives not only a constant supply of fresh water but also may be stimulated by any chemical change in the water above.

Worms occupying glass tubes respond to chemical stimulation of food as readily as those in burrows. Sea water squirted from a pipette close to a tube results in no response, but when a filtered extract of clam is introduced in the same manner the worm starts forward, moving quickly toward the end of the tube toward the juice, thrusting out its head and seizing a bit of clam dropped near the tube, or held in the forceps. This reaction was observed many times and with several individuals, and appears to be subject to remarkably little variation. By use of the glass tube every movement of the worm can be seen perfectly, and the method promises to be an excellent one for the study of the distribution of the receptors involved in the responses. Experiments designed to throw light on this aspect of the problem are already under way and will be reported upon at a later time.

SUMMARY.

1. *Nereis virens* is carnivorous, although in the absence of other food it has been observed to feed upon sea lettuce. Under natural conditions it undoubtedly is omnivorous, since Gross has found evidence of the presence of plant food in the digestive tract.

2. *Nereis* was never observed to leave its burrow when baited with meat of various marine animals, but it may expose all except the posterior segments of its body in reacting to the bait. This does not mean that the worm may not leave its burrow under other circumstances. The animal is highly thigmotactic.

3. There is positive evidence that *Nereis* depends upon a chemical sense in finding animal food; sight playing little if any part in the act. Currents in the burrow produced by an undulatory body movement are undoubtedly a factor in conveying food stimuli to the sense organs.

4. *Nereis* shows a marked tendency to extend its body from the burrow in the direction of food, and failing to reach it, to reappear in a new position nearer the source of the stimulating material.

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